

Metabolic Rates in Early Life History Stages of Elopomorph Fishes

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Abstract. The respiratory electron transport system (ETS) assay was used to estimate metabolic rates in four species of eel (Anguilliformes: Ophichthidae and Congridae) leptocephali (*Myrophis punctatus*, *Ophichthus* sp., *Hildebrandia flava*, and one unidentified congrid) and the bonefish (Albuliformes: Albulidae: *Albula* sp.). Wet-weight-specific ETS values in whole-body homogenates, assayed at physiological temperatures, ranged from 4–20 $\mu\text{g-at O h}^{-1}$ (g wet wt)⁻¹. Arrhenius activation energies (E_a) ranged from 11.0–15.7 kcal mole⁻¹. Both wet-weight-specific ETS activity and oxygen consumption rate increased approximately fivefold during metamorphosis of leptocephali of *Albula* sp. Wet-weight-specific ETS activity showed little change as leptocephali of *M. punctatus* transformed into glass eels, but increased about fivefold as glass eels metamorphosed into elvers. No significant difference was found in ETS activity measured in fresh early metamorphic leptocephali of *Albula* sp. and leptocephali that had been stored frozen at -70°C for up to 15 months. The data suggest that metabolic rates are low in leptocephali, which implies that the demand for nutrients is also relatively low. We argue that the apparent diet of these larvae seems capable of providing a sufficient supply of nutrients under these conditions.

Introduction

A leptocephalous larva is characteristic of marine teleost fishes (superorder Elopomorpha) comprising the orders

Albuliformes (including Notacanthiformes), Anguilliformes, Elopiformes, and Saccopharyngiformes (Robins, 1989). In addition to their distinct morphological characteristics, including the presence of a transparent, laterally compressed body composed mainly of a central core of gelatinous material (Smith, 1984), leptocephali differ from larvae of most other marine teleosts in having an extended larval period, referred to here as the premetamorphic period. This period, during which the leptocephalus increases in size as the gelatinous matrix is formed, may last from a few months within the albuliforms and elopiforms (Smith, 1980; Pfeiler *et al.*, 1988) to several years within the anguilliforms (Schmidt, 1925). The metamorphic period, during which the leptocephalus transforms into a juvenile fish, is usually completed within 2–3 weeks (Pfeiler, 1986). In addition to increased development of muscle, bone, and internal organs, metamorphosis is characterized by a decrease in size as the gelatinous matrix is broken down (Pfeiler, 1989).

The source of nutrition in premetamorphic leptocephali has puzzled biologists for decades. Most of the premetamorphic period is passed in the absence of a yolk sac (Pfeiler, 1986), and identifiable food material has not been observed in the gut of many species (for references see Pfeiler, 1989). The presence of a functional digestive system also has been questioned (Rasquin, 1955; Hulet, 1978). Premetamorphic leptocephali may be receiving nutrients by absorption of dissolved organic matter across surface epithelia and by ingestion of particulate organic matter and microscopic organisms (Pfeiler, 1986; Hulet and Robins, 1989; Otake *et al.*, 1993), but the relative contribution of these potential sources of nutrients has not been determined.

Most of the nutritional requirements of metamorphic leptocephali are thought to be provided by breakdown and utilization of organic material stored in the extracel-

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Abbreviations: ETS, electron transport system; NADH, reduced nicotinamide adenine dinucleotide; NADPH, reduced nicotinamide adenine dinucleotide phosphate; INT, *p*-iodonitrotetrazolium violet, E_a , Arrhenius activation energy; V_{O_2} , routine oxygen consumption rate; R:ETS, ratio of wet-weight-specific V_{O_2} to ETS activity.

lular gelatinous body matrix (Rasquin, 1955; Pfeiler, 1986). Recent work (J. Govoni, unpublished data) has revealed the presence of fecal pellets and protozoans in the gut of metamorphosing eel (*Myrophis punctatus*) leptocephali; these may also provide a nutritional source.

It follows that, if the metabolic demands of premetamorphic leptocephali are low, as might be expected given their high water content and large extracellular gelatinous component (Pfeiler, 1984; Smith, 1984), these larvae should have low energy requirements overall, and thereby be capable of subsisting on the very low concentrations of dissolved organic compounds in seawater and on minute food particles. Data on oxygen consumption could help confirm this hypothesis, but obtaining undamaged premetamorphic leptocephali for determination of metabolic rates is difficult. An alternate method of estimating respiratory rates is the electron transport system (ETS) assay, which has been used in a wide variety of marine phytoplankton, zooplankton, and micronekton (Packard, 1971; Packard *et al.*, 1975; Owens and King, 1975), as well as in specific tissues such as fish liver (Smith and Chong, 1982).

The purpose of the present study was (1) to obtain ETS activity measurements on several species of anguilliform and albuliform leptocephali (premetamorphic and early metamorphic), (2) to determine the effects of assay temperature on ETS activity of leptocephali collected at different temperatures, and (3) to determine whether changes in activity occurred during metamorphosis of albuliform (*Albula* sp.) and anguilliform (*M. punctatus*) leptocephali. We also present data on oxygen consumption rates of metamorphosing leptocephali of *Albula* sp. and compare these rates with ETS activity.

Materials and Methods

Animals

Anguilliform leptocephali were collected from 28 January–2 February 1990 in the western North Atlantic, off the coast of North Carolina, as described by Pfeiler (1991). Water temperature at the depth of collection ranged from 12–23°C. After species identification (voucher specimens were retained [Pfeiler, 1991]), leptocephali for analysis were placed in plastic vials, immediately frozen in liquid nitrogen, and stored at –70°C.

The species identified were *Hildebrandia flava* (Goode and Bean) and one unidentified species, both from the family Congridae; and *Myrophis punctatus* Lütken and *Ophichthus* sp., both from the family Ophichthidae. Specimens of *M. punctatus* were also collected on 26 January 1990 (1830–2000 h, Eastern Standard Time) and 29 January 1992 (0100–0200) at flood tide with a plankton net suspended from a small bridge at Beaufort, North Carolina. Water temperature was 9°C. These larvae were either immediately frozen or placed in an aquarium with

running seawater at ambient temperature (9–16°C) and allowed to metamorphose to glass eels and elvers and then frozen and stored at –70°C.

Metamorphosing leptocephali of *Albula* sp. (Albuliformes: Albulidae) were collected with a beach seine in the Gulf of California at Estero del Soldado, Guaymas, Sonora, Mexico, on 4 January 1990 (water temperature = 16°C), placed in plastic bags, and immediately transferred to a freezer at –18°C. They were stored for 2 weeks at –18°C and then transferred to –70°C, where they were stored until used for ETS assays. Experiments were also conducted with fresh larvae collected on 7 and 14 March 1992 (water temperature = 19 and 23°C). The first group was held in an aquarium with running seawater at ambient temperature (19–21°C) for 9 days and allowed to metamorphose to advanced larvae; the second group of early metamorphic larvae was assayed immediately.

Chemicals

The following chemicals were purchased from Sigma Chemical Co., St. Louis, Missouri: β -NADH (grade III), β -NADPH (type I), *p*-iodonitrotetrazolium violet (INT), polyvinylpyrrolidone, and Triton X-100. All other chemicals were of analytical grade. Water was glass distilled.

ETS assay

ETS activity was determined both on fresh animals (*Albula* sp. only) and on animals that had been stored at –70°C for up to 15 months. Immediately before assay, frozen fish were thawed. Both thawed and fresh fish were then rinsed with distilled water, measured (total length or standard length to the nearest millimeter), and weighed (wet weight to the nearest 0.1 mg). Individual fish were homogenized in a hand-held glass homogenizer using 10–20 ml of a cold (4°C) solution containing 75 μ M MgSO_4 , 1.5 mg/ml polyvinylpyrrolidone, and 0.2% (v/v) of Triton X-100 in 0.1 M phosphate buffer (pH 8.5) (Solution “ETS B” of Owens and King, 1975). The homogenate was centrifuged for 10 min at 7800 *g* (4°C). One milliliter of the supernatant was immediately assayed for ETS activity according to Owens and King (1975). This method is based on the reduction, and corresponding increase in absorbance at 490 nm, of an artificial electron acceptor (INT) by the respiratory electron transport system when NADH and NADPH are used as electron donors.

Assays were conducted, in duplicate, for 20 min at temperatures ranging from 10 to 30°C. Reaction mixtures were pre-incubated for 5 min at the appropriate temperature before initiating the reaction. Absorbance readings were taken immediately after stopping the reaction. Unless indicated otherwise, ETS activity refers to microgram-atoms of oxygen consumed per hour ($\mu\text{g-at O h}^{-1}$) and is expressed on a wet weight, dry weight, or individual basis.

Dry weight and water content were determined for leptocephali of *M. punctatus* (70–77 mm total length; 0.2196–0.2868 g wet weight) and *Ophichthus* sp. (77–85 mm total length; 0.2175–0.3026 g wet weight). Three individuals of each species were rinsed, measured and weighed, and then dried to constant weight in an oven at 70°C. Water contents ranged from 92.5 to 92.9% (mean = 92.7%) for *M. punctatus* and from 90.1 to 92.1% (mean = 91.2%) for *Ophichthus* sp. Mean water contents for each species were then used to estimate dry weights of larvae assayed for ETS activity. Dry weights (y) of leptocephali of *Albula* sp. were calculated from wet weights (x) using the least-squares regression equation, $y = 18.445 + 59.610x$ (Pfeiler and Luna, 1984).

Oxygen consumption

Oxygen consumption rates were determined for metamorphosing leptocephali of *Albula* sp. The respirometer consisted of a 570-ml glass jar fitted with an oxygen electrode (Yellow Springs Instruments Model 57 Oxygen Meter) and connected to an air supply. The water was thoroughly mixed with a magnetic stir bar placed underneath a nylon net screen so as not to damage the larvae. Oxygen consumption was determined on four separate groups of larvae at different stages of metamorphosis. A group of larvae (from 9 to 21 individuals) was placed in the respirometer and allowed to acclimate for 5 min in constantly aerated seawater at ambient temperature (20–25°C). Because larvae are developing rapidly, showing a daily reduction in standard length of about 10–15% (Pfeiler, 1984), and because they are easily damaged, we chose not to use longer acclimation periods. Oxygen consumption was then followed in a closed system after shutting off the air supply. After the oxygen content decreased by 20–30% (20–60 min) the water was aerated for several minutes and then measurements were resumed. The total time ranged from 2 to 3 h and the number of intervals from 4 to 6.

Larvae adapted rapidly to the respirometer, as judged by their swimming behavior, and oxygen consumption rates (routine respiration) usually agreed well between intervals. The first interval (20–35 min), however, resulted in erratic values in three of the groups, probably because of handling stress, and was omitted. Corrections were made for oxygen consumption in seawater controls (without larvae). After the experiment, larvae were measured and weighed as described above.

Results

Weight-specific ETS activity values for different species of leptocephali that had been stored frozen at –70°C ranged from about 4 to 20 $\mu\text{g-at O h}^{-1} (\text{g wet wt})^{-1}$ when assayed at temperatures corresponding to, or near, water temperatures at which larvae were collected (Table I).

When expressed on a dry weight basis, the ETS values ranged from 58 to 280 $\mu\text{g-at O h}^{-1} (\text{g dry wt})^{-1}$ (Table I). ETS activity was also determined on four fresh early metamorphosing larvae of *Albula* sp. (Table I). The mean value ($\pm$ standard deviation) for wet-weight-specific activity ($10.2 \pm 1.1 \mu\text{g-at O h}^{-1} \text{g}^{-1}$) was not significantly different at the 5% level (Student's t test) from the mean value for larvae of *Albula* sp. that had been stored frozen for 10–15 months ($14.1 \pm 3.7 \mu\text{g-at O h}^{-1} \text{g}^{-1}$; $N = 4$).

Wet-weight-specific ETS activity was determined at four temperatures (ranging from 10 to 30°C) in order to construct Arrhenius plots (not shown) for estimation of apparent activation energies (E_a). E_a values were calculated from the slopes of the regression lines. All plots were linear ($r > -0.993$). E_a values ranged from 11.0–15.7 kcal mole $^{-1}$, and different adaptation temperatures had little effect on E_a in *M. punctatus* (Table II).

Changes in wet-weight-specific ETS activity were found during metamorphosis of *Albula* sp. (Fig. 1). Larvae show a pronounced shrinkage during this period, losing about 60% of their standard length (SL) in less than 2 weeks (Pfeiler, 1984). Wet-weight-specific ETS values obtained in advanced larvae near the end of metamorphosis (approximately 25 mm SL) were about 5 $\times$ higher than those obtained for early metamorphic leptocephali (>50 mm SL). When the data were converted to dry-weight-specific ETS activity (data not shown) the values were about 3 $\times$ higher in advanced larvae than in early larvae. The regression equation relating dry-weight-specific ETS activity ($\mu\text{g-at O h}^{-1} [\text{g dry wt}]^{-1}$; y) to standard length (mm; x) was $y = 512.25 - 7.04x$; $r = -0.87$; $N = 19$. When expressed as total ETS activity per larva, a smaller (approximately twofold) increase in activity was observed during metamorphosis (Fig. 2). The difference in magnitude of increase in ETS activity in Figures 1 and 2 is due to the loss of approximately 75% of larval wet weight during metamorphosis (Pfeiler, 1984).

Changes in oxygen consumption rate in metamorphosing larvae of *Albula* sp. were similar to the changes seen in ETS activity; wet-weight-specific oxygen consumption increased more than fourfold, and oxygen consumption per larva increased about twofold (Table III). Because of a lack of ETS assay reagents, wet-weight-specific ETS activity values were calculated for the mean standard lengths of larvae used in the oxygen consumption experiments, using the regression equation from Figure 1. These data were then used to estimate the ratios of respiration to ETS activity (R:ETS) that are given in Table III.

Changes in wet-weight-specific ETS activity were also found during metamorphosis of *M. punctatus* (Fig. 3), although the pattern was different from that seen in *Albula* sp. As with *Albula* sp., metamorphosing leptocephali of *M. punctatus* shrink and lose wet weight during the transformation to glass eels. Wet-weight-specific ETS activity,

Table I

Weight-specific ETS activity in leptocephali expressed on a wet weight and dry weight^a basis

Species	Wet wt (g)	Length ^b (mm)	Temperature (°C)		ETS activity			
			Water	Assay	$\mu\text{g-at O h}^{-1} \text{g}^{-1}$		$\mu\text{l O}_2 \text{ h}^{-1} \text{g}^{-1}$	
					Wet wt	Dry wt	Wet wt ^c	Dry wt ^c
<i>Myrophis punctatus</i>	0.1915	67	23	23	20.4	280	246	3.37
	0.3008	78	9	10	4.2	58	51	0.70
<i>Ophichthus</i> sp.	0.2220	71	18	17	7.6	87	92	1.05
	0.2254	80	18	17	5.1	58	61	0.70
	0.2857	80	18	17	11.4	130	137	1.57
<i>Hildebrandia flava</i>	0.1868	59	21	24	6.9	—	83	—
	0.3225	67	21	23	5.3	—	64	—
Congridae (unidentified)	0.2983	76	23	23	9.8	—	118	—
<i>Albula</i> sp.	0.4738	56	16	17	12.5	127	151	1.53
(early metamorphic)	0.3815	53	16	23	19.2	177	231	2.13
	0.4130	53	16	23	13.9	133	168	1.60
	0.4351	55	16	23	10.7	105	129	1.27
	0.5917 ^d	56	23	23	10.7	118	129	1.42
	0.4858 ^d	58	23	23	8.8	90	106	1.08
	0.5681 ^d	56	23	23	11.3	123	136	1.48
	0.6029 ^d	61	23	23	9.9	110	119	1.33

^a Dry weights for *M. punctatus* and *Ophichthus* sp. were calculated using mean water contents of 92.7% and 91.2%. Dry weights for *Albula* sp. were calculated from wet weights (see Materials and Methods).

^b Standard length for *Albula* sp.; total length for all others.

^c $\mu\text{g-at O}$ converted to $\mu\text{l O}_2$ at 20°C ($0.083 \mu\text{g-at O} (\mu\text{l O}_2)^{-1}$).

^d Data from fresh larvae; all other larvae had been stored frozen at -70°C for periods ranging from 8 to 15 months.

however, showed only a small increase during this time. Wet weight continues to decrease during the transformation from glass eels to elvers, although total length remains about the same. For this reason, wet weight, instead of length, was used as the independent variable in Figures 3 and 4. The data in Figures 1 and 3 (and Figs. 2 and 4), can, however, be compared because standard length (x) is a linear function of wet weight (y) in metamorphosing leptocephali of *Albula* sp. ($y = -0.145 + 0.011x$; Pfeiler, 1984). It is during the transformation from glass eels to elvers in *M. punctatus* that a large increase in wet-weight-specific ETS activity was seen (Fig. 3). Total ETS activity per individual decreased about twofold during metamor-

phosis of *M. punctatus* (Fig. 4), in contrast to the twofold increase in *Albula* sp. (Fig. 2).

Discussion

Wet-weight-specific ETS values reported here for leptocephali of four anguilliform species and one albuliform agree well with those reported by Schalk (1988) for unidentified leptocephali that had not been frozen and were analyzed within 12 h of capture. This suggests that freezing larvae in liquid nitrogen immediately after capture, followed by storage at -70°C for up to 15 months, resulted in little or no loss in ETS activity. In addition, we found no significant difference in ETS activity values between fresh and frozen early metamorphic leptocephali of *Albula* sp. (Table I; Figs. 1 and 2). The latter group, although stored at -70°C , was not quick frozen in liquid nitrogen (see Materials and Methods). The sample size for fresh advanced metamorphic larvae of *Albula* sp. is too small ($N = 2$) for statistical comparison, but ETS activity values did not differ substantially in fresh larvae compared with frozen larvae (Figs. 1 and 2).

Yamashita and Bailey (1990) also found that cold storage had little effect on ETS activity in larval walleye pollock (*Theragra chalcogramma*); they reported about a 10% loss in activity after 50 days at -80°C . Substantial loss

Table II

Apparent Arrhenius activation energies (E_a) for ETS activities in leptocephali

Species	Water Temp. (°C)	E_a (kcal mole ⁻¹)
<i>Albula</i> sp.	16	11.0
<i>Hildebrandia flava</i>	21	12.2
<i>Ophichthus</i> sp.	18	12.4
<i>Myrophis punctatus</i>	12	14.9
<i>Myrophis punctatus</i>	21	15.7

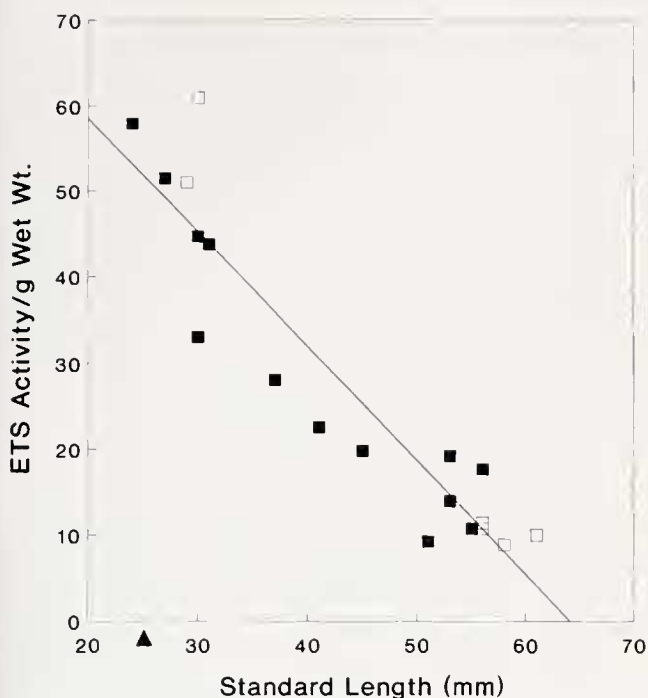


Figure 1. Change in wet-weight-specific ETS activity ($\mu\text{g-at O h}^{-1} [\text{g wet wt}]^{-1}$) during metamorphosis of bonefish (*Albula* sp.) leptocephali ($y = 85.13 - 1.33x$; $r = -0.93$; $N = 19$). Assay temperature = 23°C . Metamorphosis proceeds from right to left along the x axis because larvae decrease in length during this period (Pfeiler, 1984). The arrowhead shows the standard length at the end of metamorphosis. Open symbols are values obtained from fresh larvae; solid symbols are values obtained from frozen larvae (see Materials and Methods).

of activity would, however, be expected in damaged larvae, whether they were assayed immediately or frozen. Pelagic premetamorphic leptocephali are often dead or dying by the time the net is retrieved, and this might explain some of the variation in activity values reported here and by Schalk (1988).

The apparent activation energies (E_a) for ETS activity of leptocephali and the lack of an effect of environmental temperature on E_a in *M. punctatus* agree well with results reported for marine plankton (Packard *et al.*, 1975).

Wet-weight-specific ETS values for leptocephali reported here and by Schalk (1988) ($4\text{--}20 \mu\text{g-at O h}^{-1} \text{g}^{-1}$ at *in situ* temperature) are very low compared to those reported for walleye pollock larvae by Yamashita and Bailey (1990). These authors found an ETS value of $5.82 \mu\text{O}_2 \text{ h}^{-1} (\text{mg dry wt})^{-1}$ in prefeeding larvae assayed at 6.5°C . Mean ETS activity of the four fresh early metamorphic leptocephali of *Albula* sp. (Table I) was about 4 times lower ($1.33 \mu\text{O}_2 \text{ h}^{-1} (\text{mg dry wt})^{-1}$) for larvae adapted to, and assayed at, a much higher temperature (23°C). If we ignore the possibility of compensation to low temperature adaptation and assume that E_a for *Albula* sp. is not affected by adaptation temperature, the value obtained at 23°C can be converted to 6.5°C using the

equation given in Båmstedt (1980). The result ($0.44 \mu\text{O}_2 \text{ h}^{-1} (\text{mg dry wt})^{-1}$) is more than 10-fold lower than that found in larval walleye pollock. Part of this decrease may be a function of size differences between species; dry weights of leptocephali of *Albula* sp. were about 10^3 greater than those of larval walleye pollock. Yamashita and Bailey (1990) found in pollock, however, that ETS activity per individual larva is directly related to dry weight over a 10-fold range of weight. In addition, hepatic ETS activity in American plaice (*Hippoglossoides platessoides*) is a function of liver wet weight to the 0.86 power (Smith and Chong, 1982). These results suggest that differences in weight could, at most, account for only a two- to threefold decrease in ETS activity in *Albula* sp. compared with walleye pollock.

Because ETS activity is assumed to represent the maximum potential oxygen consumption rate (Owens and King, 1975), it follows that metabolic rates in leptocephali, expressed on a wet weight or a dry weight basis, are also low when compared with other fish larvae. This conclusion is valid only if the ratios of respiratory rate (R) to ETS activity (R:ETS ratio) are similar in both groups. The R:ETS ratios in leptocephali of *Albula* sp. (Table III) agree well with values reported for prefeeding and feeding larval walleye pollock, 0.27 and 0.47, respectively (Yamashita and Bailey, 1990). Early and intermediate metamorphosing leptocephali of *Albula* sp. (first two groups

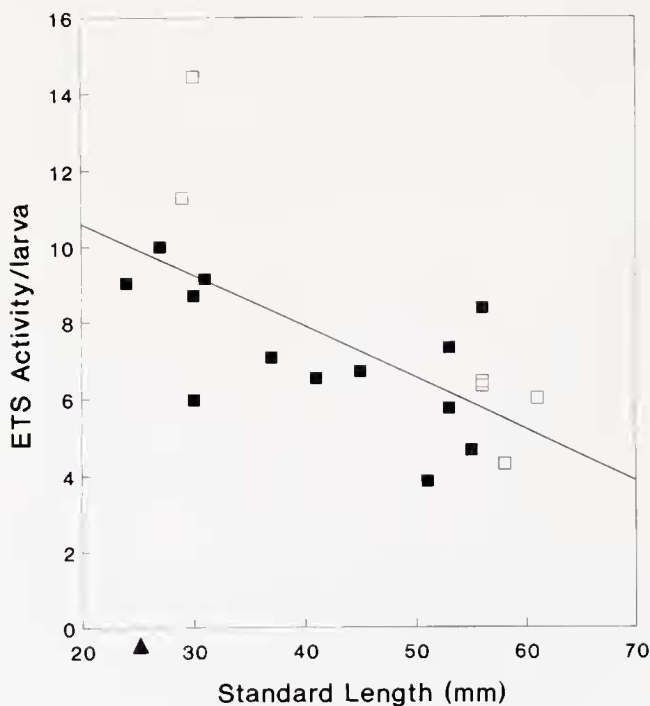


Figure 2. Change in total ETS activity ($\mu\text{g-at O h}^{-1}$) during metamorphosis of bonefish (*Albula* sp.) leptocephali ($y = 13.30 - 0.14x$; $r = -0.67$; $N = 19$). Assay temperature = 23°C . Same symbols as in Figure 1.

Table III

Oxygen consumption ($\dot{V}_{O_2}$) in metamorphosing *Albula sp. leptocephali*

SL ^a (mm)	N ^b	Total WW ^c (g)	Temp. (°C)		$\dot{V}_{O_2}$ ($\mu\text{l O}_2 \text{ h}^{-1}$)		R:ETS ^d
			Run	Adapt.	per larva	per g WW	
49.4 (± 3.0)	9	3.9186	24–25	23	29.6	67.9	0.29
39.8 (± 3.7)	21	7.2587	20–21	19	31.3	90.6	0.23
33.4 (± 1.8)	21	5.2984	21–22	20	45.6	180.6	0.37
28.2 (± 0.8)	20	4.0744	24–25	21	57.3	281.1	0.49

^a Mean standard length ($\pm$ standard deviation).^b N = total number of larvae in respirometer during the run.^c WW = wet weight.^d Ratio of wet-weight-specific $\dot{V}_{O_2}$ (R = respiration) to ETS activity (see Results).

in Table III; mean R:ETS = 0.26) are nonfeeding; the more advanced metamorphosing larvae (last two groups in Table III; mean R:ETS = 0.43) are just beginning to feed. In general, the R:ETS ratio shows species-specific differences with values of 0.50 or less (Owens and King,

1975; Schalk, 1988). In spot (*Leiostomus xanthurus*) and Atlantic menhaden (*Brevoortia tyrannus*) larvae, this ratio can be as low as 0.10 (P. Tester and L. Coston-Clements, pers. comm.).

In order for ETS activity to be of value in precisely estimating metabolic rates, the relationship between respiration and ETS activity must be determined for each species. Clearly, this is not possible for organisms that are often dead on capture. However, based on the good agreement of R:ETS ratios in larval walleye pollock and metamorphosing *Albula sp. leptocephali*, we suggest that ETS values can also be used to obtain rough estimates of res-

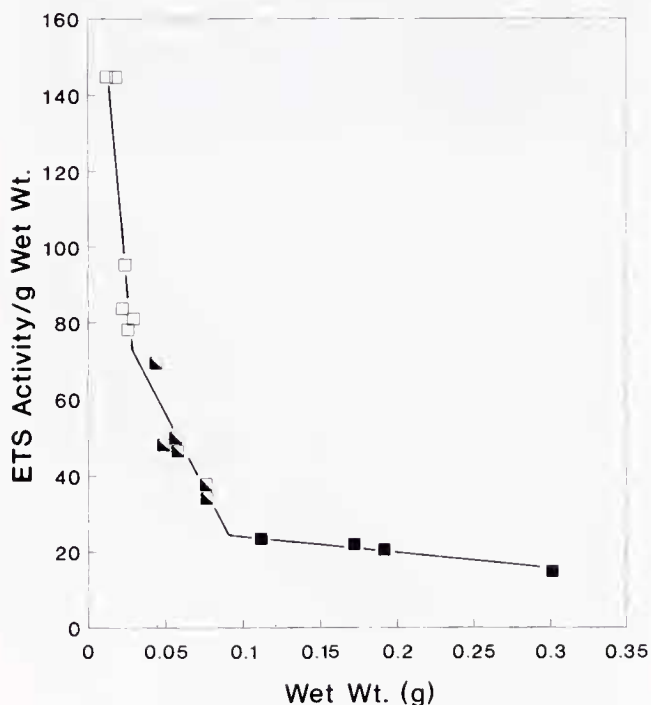


Figure 3. Change in wet-weight-specific ETS activity ($\mu\text{g-at O h}^{-1} [\text{g wet wt}]^{-1}$) during metamorphosis in the eel, *Myrophis punctatus*. Assay temperature = 23°C. Metamorphosis proceeds from right to left along the x axis (key to symbols: solid = leptocephali; solid/open = glass eels; open = elvers). The four leptocephali, in order of decreasing wet weight, measured 78, 67, 63 and 55 mm total length; total length of glass eels and elvers ranged from 43 to 49 mm and was not related to wet weight. Regression equations are as follows: (leptocephali) $y = 29.21 - 47.27x$; $r = -0.99$; $N = 4$; (glass eels) $y = 94.68 - 792.58x$; $r = -0.88$; $N = 6$; (elvers) $y = 205.56 - 4658.42x$; $r = -0.88$; $N = 6$. All data were obtained from frozen individuals (see Materials and Methods).

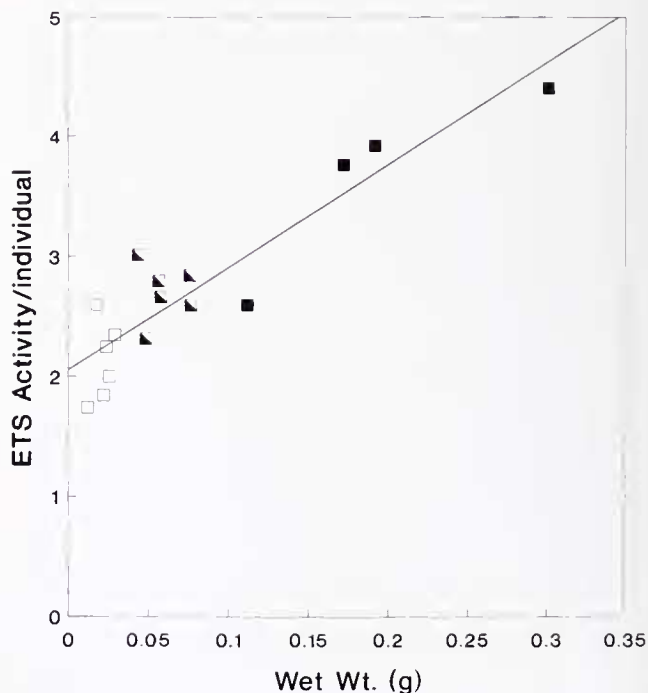


Figure 4. Change in total ETS activity ($\mu\text{g-at O h}^{-1}$) during metamorphosis in the eel, *Myrophis punctatus* ($y = 2.05 + 8.53x$; $r = 0.91$; $N = 16$). Assay temperature = 23°C. Same symbols as in Figure 3.

piration and, therefore, that the low ETS values obtained in premetamorphic leptocephali in this study and by Schalk (1988) indicate a low metabolic rate compared with other marine teleost larvae. The prediction would be false only if the R:ETS ratio in leptocephali was much higher than in other fish larvae, and our data suggest that it is not.

Oxygen consumption rates of early metamorphic leptocephali of *Albula* sp. (mean standard length = 49.4 mm; Table III) compare favorably with the low metabolic rates of larval lampreys of approximately the same size (Lewis and Potter, 1977), if one assumes a Q_{10} of 2 to account for differences in experimental temperature. The values for lampreys, however, represent standard respiration (*i.e.*, no activity), as compared to routine respiration (*i.e.*, minimal swimming activity) for *Albula* sp., which offers further support for the view that metabolic rates are low in leptocephali. Wet-weight-specific oxygen consumption rates increase during metamorphosis of larval lampreys (Lewis and Potter, 1977), a pattern similar to that seen in *Albula* sp. and *M. punctatus* (Figs. 1 and 3).

A low metabolic rate in leptocephali would result in a lower demand for nutrients and offer an overall survival advantage to the long-lived premetamorphic larval stage. Under these conditions the seemingly inefficient, putative feeding strategies described earlier may be capable of supplying all the nutritional requirements of these larvae.

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